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MONTHLY REPRODUCTIVE CYCLES IN THREE SYMPATRIC HOOD-BUILDING TROPICAL FIDDLER CRABS (GENUS *UCA*)

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Since the early studies of Korringa (1947), several intertidal invertebrates have been reported to exhibit semi-monthly cycles of reproductive activity (see Neumann, 1975; Klapow, 1976). Included in these studies are several utilizing fiddler crabs (genus *Uca*) (Crane, 1958; Feest, 1969; von Hagen, 1970; Zucker, 1976; Christy, 1978). This paper confirms and quantifies the reported cyclicity of reproductive activity in *Uca* but reveals a monthly (rather than semi-monthly) cycle tied to a specific lunar phase in three tropical *Uca* species. Male courtship activity reached significant peaks during the spring tides occurring after the Full Moon (FM).

Surface activity (which includes courtship, feeding, and combat) for these intertidal crabs is restricted to low-tide periods. Temperate species hibernate in the winter (Crane, 1943), but males court (*i.e.,* wave their major cheliped) throughout all low-tide periods in the warmer months (Salmon, 1965). Subtropical species, exposed to longer periods of warm weather, court only during diurnal and early evening low-tide hours (Salmon and Atsaides, 1968). Tropical species court in the daytime throughout the year but have only rarely been reported to court at night (Crane, 1975). Many tropical species do not even leave their burrows during nocturnal low tides (personal observation). Thus, there is an inverse relationship between the number of warm months in a given region, and the amount of time devoted to courtship activities on a daily basis.

Observations by Crane (1958) in Trinidad on *U. maracoani,* by Feest (1969) on *U. annulipes* and *U. triangularis* in South India, by von Hagen (1970) on four Trinidad species, by Christy (1978) on *U. pugilator* in Florida, and my own earlier work on *U. musica terpsichores* in Panama (Zucker, 1973, 1976) suggested a further reduction in the daily hours of courtship in tropical forms. Courtship in *U. maracoani* was restricted to those low-tide periods coinciding with early morning hours (Crane, 1958). In *U. annulipes* and *U. triangularis,* waving peaked between 1000 to 1100 hr (Feest, 1969). Four of the seven *Uca* species found on Trinidad were observed by von Hagen (1970) to restrict courtship activities to low tides occurring around the Full Moon (FM) and New Moon (NM) (late morning hours). Christy (1978) found courtship most prevalent in *U. pugilator* during the week following each Quarter Moon. In *U. m. terpsichores* courtship occurred during late morning through mid-afternoon low-tide periods, *i.e.,* during FM and NM spring tides (Zucker, 1973, 1976). Other diurnal low-tide periods were devoted to feeding, burrow repair, aggression, wandering or remaining within the burrow. Since the low-tide period occurs approximately 50 min later each day, about 15 days pass before low tide again coincides with the observed hours of courtship activity. Hence, it appears from these studies that male *Uca* were exhibiting semi-monthly cycles of courtship and other activities and were perhaps synchronizing their daily behavior patterns with one another (Crane, 1958; Barnwell, 1968; Zucker, 1976). Recent evidence suggests that females of some *Uca* species are reproductively receptive mainly around the FM period (von Hagen, 1962; Zucker, 1973) while other species exhibit peaks in receptivity twice each month (von Hagen, 1970; Christy, 1978).

Although all previous studies revealed a semi-monthly rhythm of male courtship activity, these studies were, for the most part, either nonquantitative or dealt with small sample sizes. Crane's (1958, 1975) most extensive work in this area involved six male *U. maracoani* in an artificial outdoor "crabbery" in Trinidad. To confirm and extend Crane's observations, the amount of time individually-marked male *U. m. terpsichores* spent performing various behaviors on a daily basis was recorded in the field starting 1 hr past dead low tide (Zucker, 1973, 1976). This study, too, suffered from a small sample size (only five males and no females were monitored each day). Feest (1969) merely described general impressions of when courtship peaked in her study populations, and von Hagen (1970) indicated days in which more or less than 50% of the males were courting.

The present work utilized the three sympatric Panamanian hood-building (formerly, shelter-building) species as part of a larger investigation of the social organization of these crabs. This paper examines the degree of synchronization of behaviors within these species in order to ascertain the timing of courtship and other activities within the lunar month in a quantitative manner.

Crane (1941) originally used the term "shelter" to describe the semi-domes of mud some males constructed over the mouth of their burrows. In her recent major work, Crane (1975) has adopted the term "hood" which was previously used by Matthews (1930). The term "hood" is more neutral in connotation than "shelter" which implies a function for these structures. Although some previous workers assumed they functioned to protect or shelter the crabs from the sun (Matthews, 1930), recent work has shown that they function in a social context. Zucker (1974; and in preparation) has shown that the presence of hoods serves to reduce the size of a male's territory since he only courts in front of it rather than in a 360° circle around his burrow as non-hood owners do. This reduction in courtship area lowers the amount of overlap between neighboring territories. Aggressive encounters are likewise reduced (Zucker, in preparation). Von Hagen (1968, 1972) suggested hoods might attract females to the males' burrows. This possibility will be tested in the future.

Materials and Methods

Observations were made from July 19 to August 14, 1975, on an intertidal muddy-sand flat in the Panama Canal Zone. The flat, along the east bank of the Pacific entrance to the Canal, is the same one described by Crane (1941) as housing 15 species of *Uca*. The upper flat was less muddy than the remainder. This muddy-sand area was inhabited mainly by the three Panamanian "hood-builders," *U. musica terpsichores, U. latimanus* and *U. beebei.*

Three "permanent" transects were placed in the muddy-sand region, each of which contained predominantly one of the three species. Each transect was marked by sinking four 1.52 m × 1.27 cm steel rods into the ground about 1.45 m. Nylon cord was tied around these posts during observations each day. The *U. m. terpsichores* transect was uppermost on the flat and measured 66 cm × 625 cm (4.13 m^2). The *U. latimanus* transect, located 5.40 m below and 15.66 m to the west side of the *U. m. terpsichores* one, was originally 75 cm × 658 cm (4.94 m^2). It was changed to 70 cm × 542 cm (3.79 m^2) after the rods were dislodged by wave action on July 21. The *U. beebei* transect, located 3.6 m below the *U. latimanus* one, was initially 75 cm × 625 cm (4.69 m^2). It was enlarged to 145 cm × 678 cm (9.83 m^2) after these rods were also dislodged on July 21. The *U. beebei* transect was made considerably larger than the others in order to compensate for the lower density of males in that population (see Fig. 1). No other rod dislodgements occurred during the course of the study. Observations were made 3 m from each transect.

Each day, starting at low tide and again at one hour past dead low tide, the "instantaneous" behavior of each individual within the three transects was recorded (see Altmann, 1974). These hours included the height of courtship activity. Males perform a daily sequence of behavior patterns starting with emergence from their burrows several hours before dead low tide. If courtship activity occurs during a given low-tide period, it will not be evident until about the hour of dead low tide. Each transect was scanned with the aid of binoculars. A verbal description of the species, sex, possession of a hood, and behavior of each individual at the moment of observation was recorded on a tape recorder for later transcription. The behaviors recorded included: feeding, waving (the major cheliped), waving-and-feeding (simultaneous waving motion by major cheliped and feeding motion by minor cheliped), combat, staying "in burrow" (recorded when a hood but no crab was present or a crab was seen leaving its burrow during the scan), digging, wandering, cleaning (sand off crab's carapace) and standing still. Each transect scan took from 2 to 10 min depending upon the number of crabs active, the behaviors being performed and the number of disturbances from predators. The order in which the transects were scanned was randomized from day to day.

The data were organized according to the hour of low tide rather than on a daily basis. This method was chosen to facilitate comparisons with past and/or future work. During several hourly intervals (0900–0959 hr, 1100–1159 hr after the FM, and 1100–1159 hr after the NM) the tidal advance slowed enough so that low tide on two consecutive days occurred during the same hourly interval. When this happened, the data were averaged for the two days. The results from the two hourly scans are fairly similar. The one hour past low-tide set of data is reported here in order to compare it to earlier work (Zucker, 1973, 1976) which was also based on observations made one hour past low tide.

Results

The results of the scan samples reveal a concentration of courtship activities during the days just after the FM for all three species.

Figure 1 shows the observed density of active males and females, respectively, for each species at one hour after low tide for each low-tide hour. For example,

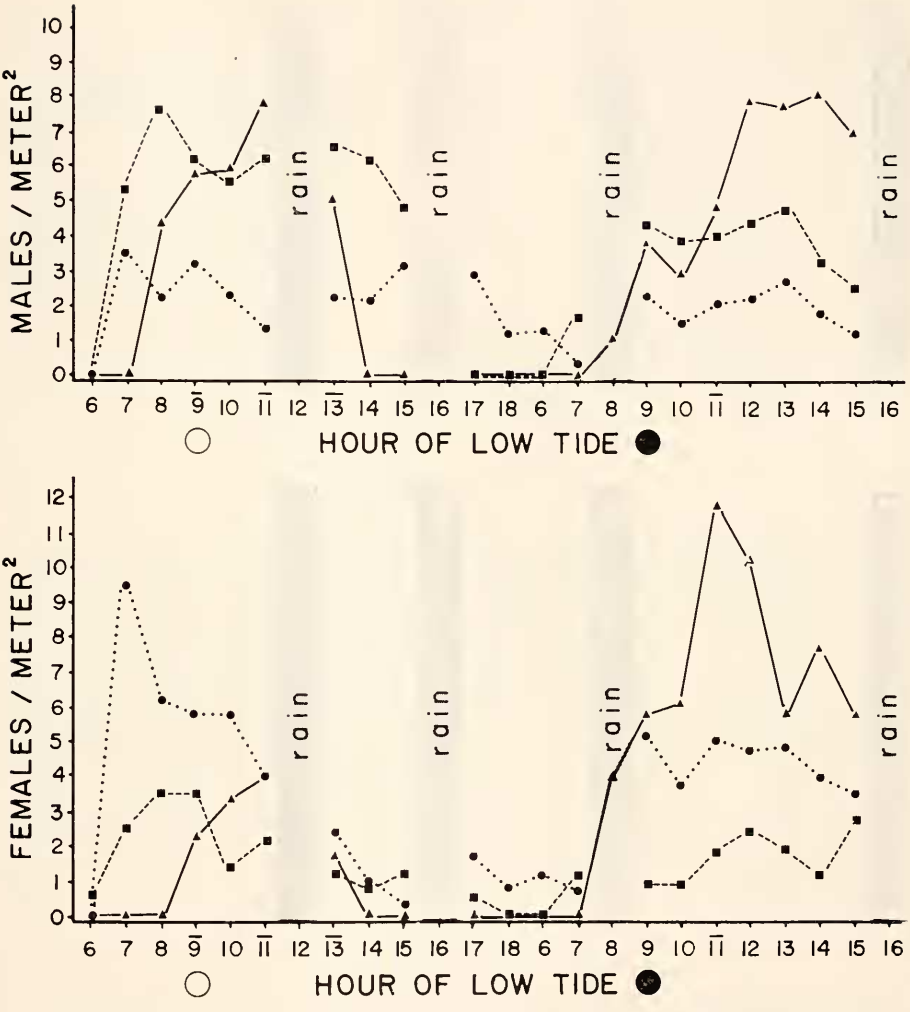
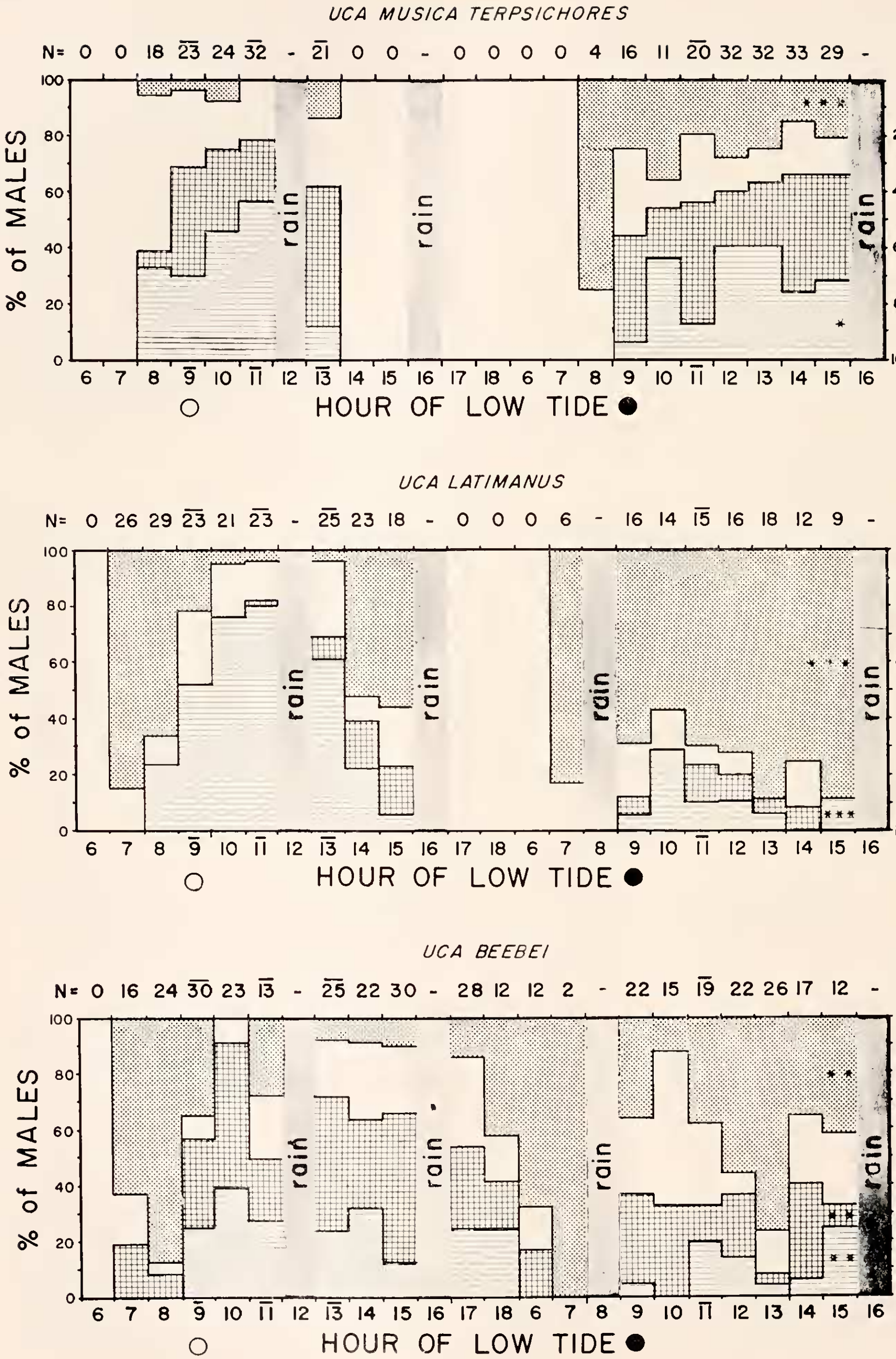


FIGURE 1. The density of male and female *Uca musica terpsichores* (triangles), *U. latimanus* (squares), and *U. beebei* (circles) observed on the surface of their respective transects, as a function of low tide hours. Hours in which two consecutive low tides occurred during that hourly interval are represented by an "average" bar over the hour on the abscissa. Data were gathered from July 19 to August 14.

low tide on July 24 occurred between 1000 hr and 1059 hr (represented as 10). The actual observations on that day were made about 1 hour later. The precise density of crabs in each transect could not be determined since some individuals may have been temporarily within their burrows as the transect was scanned. Male *U. m. terpsichores* densities reached peaks several days after both the FM and NM. Male *U. latimanus* density was about the same as *U. m terpsichores* during the FM period but only about half that many emerged during the NM


UCA MUSICA TERPSICHORES
N= 0 0 18 23 24 32 - 21 0 0 - 0 0 0 0 4 16 11 20 32 32 33 29 -
% of MALES
rain
rain
rain
HOUR OF LOW TIDE
UCA LATIMANUS
N= 0 26 29 23 21 23 - 25 23 18 - 0 0 0 6 - 16 14 15 16 18 12 9 -
% of MALES
rain
rain
rain
rain
HOUR OF LOW TIDE
UCA BEEBEI
N= 0 16 24 30 23 13 - 25 22 30 - 28 12 12 2 - 22 15 19 22 26 17 12 -
% of MALES
rain
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HOUR OF LOW TIDE

period. Male *U. beebei* density was at most only about half that of the other two species during their peaks. However, *U. beebei* density dropped to zero only during the early morning low-tide hours, while *U. m. terpsichores* and *U. latimanus* males stopped emerging in the late afternoon period as well (Fig. 1). Females of all three species were rarely observed from several days after the FM to just before the NM. Most *U. latimanus* and *U. beebei* females were observed on days just prior to the FM; *U. m. terpsichores* females were seen mainly after the NM (Fig. 1).

The days on which population densities dropped to zero parallel fairly closely the days on which the previous high tide did not cover the particular transect. Of the three transects, only the *U. beebei* transect was low enough in the intertidal zone to be covered by each high tide. The *U. latimanus* transect was covered by high tide from 0800 to 1600 hr during the FM period and from 0700 hr onwards during the NM period. Thus, there were five days in which high tide did not reach this transect. The highest transect (*U. m. terpsichores*) was covered by high tide from 0900 to 1200 hr around the FM and from 0800 hr onward around the NM. Thus, this transect was exposed at high tide during 11 of the 27 days of the study.

The percentage of male *U. m. terpsichores*, *U. latimanus* and *U. beebei* performing each of three main activities (feeding, waving, or waving-and-feeding) relative to the number of active conspecific males each hour of low tide is shown in Figure 2. The blank area on each graph represents all other activities: mainly those male crabs seen just emerging from their burrows (recorded as "in burrow") as well as a small amount of combat, cleaning, digging, standing still or wandering. Courtship (waving, and waving-and-feeding) peaked during the spring tides several days after the FM in all three species. Only in *U. m. terpsichores* was courtship also fairly prominent after the NM. Feeding was more prominent during the week surrounding the NM in all three species (Fig. 2). A chi-square test was used to compare the frequency of each of the three main behaviors and all other behaviors during the FM *vs.* NM weeks for each species (Table I). For all three species, significantly more males were waving, while significantly fewer males were feeding, around the FM than the NM ($P < 0.05$). Only in *U. beebei* were there significant differences from one week to the other for waving-and-feeding and for all other activities (other).

U. latimanus males exhibited the strongest population synchrony of activities (Fig. 2). For example, fully 80% of the active males were waving during the 1100 hr low tide period following FM (includes two consecutive days) (Fig. 2). Nearly 60% or more of the *U. latimanus* fed each day during the week following the NM (Fig. 2). Waving-and-feeding was more prominent in *U. m. terpsichores* and *U. beebei* than in *U. latimanus*. If all courtship activities (waving and waving-and-

FIGURE 2. Percentage of male *Uca musica terpsichores*, *U. latimanus* and *U. beebei*, respectively, performing various behaviors during each low tide hour. An "average" bar over a low-tide hour represents hours in which two consecutive low tides occurred during that hourly interval. Dotted area is percentage of males feeding, lined area is percentage waving, cross-hatched area is percentage waving-and-feeding and blank area is percentage in burrow or performing other infrequent activities. The asterisks on the right indicate significant differences in the number of males performing each behavior during the FM period *vs.* the NM period ($* = P < 0.05$; $** = P < 0.01$; $*** = P < 0.001$).

TABLE I

The number of male Uca m. terpsichores, U. latimanus *and* U. beebei *in each activity during the weeks of the full moon (FM) and new moon (NM) (low tides from 0600–1100 hr and 1300–1500 hr). No data were collected for FM 1200 hr, or after 1500 hr following the NM. Therefore, the corresponding data from the other moon phase period were deleted from the test.*

Behavior	*U. m. terpsichores*			*U. latimanus*			*U. beebei*		
	FM	NM	*P**	FM	NM	*P*	FM	NM	*P*
Feeding	7	34	<0.001	71	68	<0.001	53	58	<0.01
Waving/feeding	34	49	>0.50	10	5	>0.90	65	25	<0.01
Waving	45	36	<0.05	74	8	<0.001	37	8	<0.01
Other**	32	26	>0.10	33	9	>0.10	28	34	<0.02
Total	118	145		188	90		183	125	

* A two-tailed chi-square test was used to compare NM with FM period for each behavior.
** Includes: "in burrow," combat, digging, cleaning carapace, standing still, and wandering.

feeding) are pooled for *U. m. terpsichores* and *U. beebei,* strong population synchrony of courtship is also seen in these species during the FM period (Fig. 2).

The frequency of hood-building by each of the three species is shown in Figure 3. Only about 15% of all *Uca* species have been observed to build these structures (Crane, 1975). Of the 29 Panamanian species only the three reported here display this behavior. All three species restricted building mainly to a few days following the FM. A few hoods were also constructed after the NM. *U. latimanus* males again displayed the greatest synchrony. During peak construction days 83 to 100% of the *U. latimanus* males built hoods.

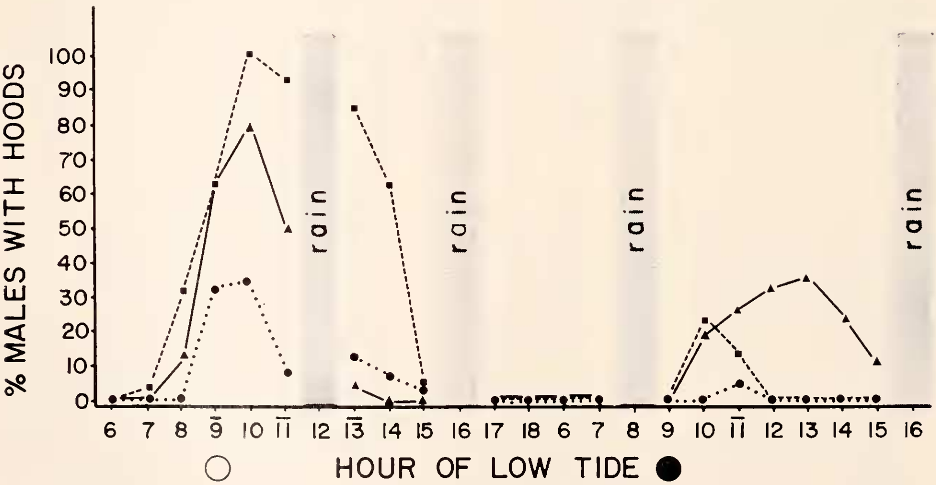

FIGURE 3. Percentage of male *Uca musica terpsichores* (triangles), *U. latimanus* (squares), and *U. beebei* (circles) building hoods each low tide hour. An "average" bar over a low-tide hour represents hours in which two consecutive low tides occurred during that hourly interval.

TABLE II

A composite of the various behavior patterns performed by males of the three Uca *species from July 19 to August 14, 1975 (low tides from 0600–1800 hr; 0600–1500 hr). All observations were made approximately one hour after low tide.*

Behavior of ♂♂	*U. m. terpsichores* N = 368 (%)	*U. latimanus* N = 380 (%)	*U. beebei* N = 457 (%)
Feeding	57 (15.49)	167 (43.95)	155 (33.92)
Waving/feeding (W/F)	114 (30.98)	20 (5.26)	131 (28.67)
Waving	117 (31.79)	129 (33.95)	77 (16.85)
Threat & combat	30 (8.15)	8 (2.11)	21 (4.60)
Other*	50 (13.59)	56 (14.74)	73 (15.97)
All feeding activities (W/F and feeding)	171 (46.47)	187 (49.21)	286 (62.58)
All courtship activities (W/F and waving)	231 (62.77)	149 (39.21)	208 (45.51)
Hood-building	111 (30.16)	163 (42.90)	35 (7.66)

* Includes: "in burrow," digging, wandering, cleaning carapace, and standing still.

Table II is a composite of the number of males performing each activity for the entire observation period from July 19 to August 14. Over the entire month's observations, more than 350 males were observed for each species. The percentage of males performing each behavior varied between species. Compared to the other two species, less than half as many *U. m. terpsichores* males fed at this time each day over the entire period. The number of males engaged in waving was about the same for *U. m. terpsichores* (32%) and *U. latimanus* (34%); only half as many *U. beebei* engaged in waving (17%). However, fewer *U. latimanus* males were engaged in all courtship activities (waving and waving-and-feeding) than the other two species. Combat was rarely seen in all three species: 8% for *U. m. terpsichores;* 2% for *U. latimanus;* and 5% for *U. beebei.* The percentage of *U. latimanus* males building hoods was higher than their percentage of waving males. This occurred since some of the hood-builders were in their burrows either briefly or perhaps with a female while the scan was being taken. Almost as many *U. m. terpsichores* built hoods as waved; only half as many *U. beebei* males constructed

TABLE III

Correlations between the frequency of each of the three main behavior patterns with hood-building (N is the number of days on which males were active.)

	U. m. terpsichores N = 16		*U. latimanus* N = 19		*U. beebei* N = 21	
	r	*P**	r	*P*	r	*P*
Hood-building *vs.*						
Feeding	−0.56	<0.05	−0.93	≪0.001	−0.45	<0.05
Wave/feed	−0.06	≫0.10	−0.16	≫0.10	0.37	>0.10
Waving	0.74	<0.01	0.95	≪0.001	0.55	<0.05

* Two-tailed test (Diem and Lentner, 1970).

hoods as waved. The relationship between feeding or courtship and hood-building for all three species is clearly seen from the correlation coefficients (Table III). In all three species there is a significant positive correlation between the number of males waving and the number of hoods constructed as well as a significant negative correlation between feeding and construction. *U. latimanus* exhibits the strongest correlations, while *U. beebei* exhibits the weakest.

A graph showing female behavioral activity is not included since most of their activities are difficult to monitor by the scan sample technique. Except for feeding, female activities take place away from the burrow entrance. These behaviors include mostly wandering (a presumed indicator of female sexual receptivity; Crane, 1975) and remaining in her own burrow, or in a male's burrow (presumably for mating). Of all the females observed, 94%, 92%, and 95% of *U. m. terpsichores* (N = 350), *U. latimanus* (N = 148), and *U. beebei* (N = 799), respectively, were seen feeding during the daily scans. One female *U. m. terpsichores,* three *U. latimanus* and four *U. beebei* were seen wandering. All but one of these eight females wandered between 1000 to 1300 hr after either the NM (two females) or FM (five females). Five matings were observed on the surface during the *U. beebei* scans. They occurred at the following times: two at 1300 hr after the FM, and one each at 0600 hr, 1000 hr, and 1500 hr during the NM week.

Discussion

This study examined the rhythmic behavior of several species of tropical fiddler crabs under natural field conditions. Early behavioral studies concerning rhythmic activity in *Uca* concentrated on the locomotory activity of crabs in laboratory containers (see Palmer, 1973, for review). Recent studies have revealed a far greater variability within a population than was previously indicated. Some individuals exhibited tidal rhythms, others diurnal rhythms and still others no apparent rhythm at all (Zucker, 1973; Lehmann, Neumann, Kaiser, 1974; Rawson and DeCoursey, 1976). Since so much variability does exist, the degree of synchrony within a population is of interest. Furthermore, studies of rhythmic activity performed under natural field conditions might shed some light on the adaptive significance of rhythmic cycling for the crabs.

Previous studies suggested that courtship activity by tropical males cycled on a semi-monthly basis (Crane, 1958; Feest, 1969; von Hagen, 1970; Zucker, 1976). Two of these studies (Crane, 1958; and von Hagen, 1970) used a criterion of 50% or more of the males waving to indicate courtship peaks. Using this criterion and pooling all courtship activities (waving and waving-and-feeding) only *U. m. terpsichores* in this study shows semi-monthly peaks of courtship. Previous work with *U. m. terpsichores,* which utilized a different method of observation, showed courtship activity occurring about equally after both the FM and NM (Zucker, 1973, 1976). However, the present study revealed that significantly more males were courting around the FM than the NM in all three species. Also, the degree of synchrony during peak courtship periods was far better than 50%. In all three species 78% or more of the adult males were engaged in courtship activities (waving and waving-and-feeding) during the same low tide period, one to three days following the FM. Nevertheless, in the present study, *U. m. terpsichores* males showed considerable courtship after the NM. This species, too, was the only one of the three in which as many males emerged several days after the NM as the FM. Thus, while *U. latimanus* and *U. beebei* males exhibited a distinct monthly cycle of courtship activity, *U. m. terpsichores* tended toward a semi-monthly cycle.

The relatively large amount of courtship activity performed by specimens of *U. m. terpsichores* following the NM may be explained by their location in the upper-most part of the intertidal zone. As shown in Figure 1 and mentioned in the results, the crabs did not emerge when the previous high tide did not cover them, which occurred around the neap tides. Apparently, during those days the dry substrate forced these semi-aquatic animals into estivation. Consequently, *U. m. terpsichores* was active only 7 days (the 2 rainy days also inhibited activity) during the 2 weeks around the FM, while the lowest of the three species, *U. beebei,* was active a full thirteen days during the same period (Fig. 2). Courtship activity during the NM period by male *U. m. terpsichores* may have compensated for the short activity period available to them during the FM weeks. Also associated with the relatively few active days available to *U. m. terpsichores* during the FM period is the greatly reduced amount of feeding at this time compared to the other two species. Peak feeding periods are early morning hours on days preceding both the FM and NM for *U. latimanus* and *U. beebei* but only before the NM for *U. m. terpsichores*. Over the entire month of observation, only 15% of the *U. m. terpsichores* males engaged in pure feeding activity, while more than twice that percentage did so in the other two species (Table II).

The reduced feeding activity by *U. m. terpsichores* may be due to any of several factors. *U. m. terpsichores* is the smallest of the three species and may, therefore, require less food for maintenance. More likely it "catches-up" on feeding by waving-and-feeding more frequently than the other two species (Table II). It may also engage in more feeding at times other than when observations were made. Agonistic activities are also usually confined to the early hours of the low-tide periods, especially on those days in which courtship will later predominate. Thus, the small amount of agonistic activities (as revealed in Table II) is somewhat misleading. When the males first emerge after the tide recedes they are cryptically colored and usually engage in some feeding. If courtship will take place later in the period, much aggression occurs presumably to secure an area for display free of other crabs, both males and females (Zucker, 1977). Once courtship starts (when these data were obtained) the females have been displaced from the males' display grounds and the males are well spaced; little aggression occurs.

One additional behavior, hood-building, was highly synchronized within the male populations. The greatest hood-building activity took place during several days just after the FM, coinciding with peak courtship activity in all three species (Figs. 2 and 3, Table III). Of the three species, only *U. latimanus* exhibited a near perfect correlation between pure courtship (waving only) and hood-building (Table III). In fact, virtually all courting *U. latimanus* males constructed hoods earlier in the low-tide period. *U. beebei* showed the smallest ratio of hoods to courting males, with *U. m. terpsichores* intermediate (Table III). In other words, in all three species only courting males build hoods, but only in *U. latimanus* is hood possession an integral part of courtship. A fuller account of the function of hoods is given elsewhere (Zucker, 1974; and in preparation). Hence, feeding, courtship, and hood-building activities were synchronized among males in all three species. *U. latimanus* males showed the greatest degree of synchrony and *U. beebei* the least.

Barnwell (1968) suggested that differences in the timing of courtship between species might act as a species isolation mechanism. He based this idea on Crane's (1958) observation that primitive species courted earlier in the morning than advanced species. Since all three species in the present study courted at the same time and were found intermingling on the same flat, limited courtship periods probably do not serve as an isolation mechanism here. The number of receptive females in a population and their reproductive behavior are probably two important factors. The ratios of males to females observed in this study for *U. m. terpsichores, U. latimanus* and *U. beebei* were 1.1:1, 2.6:1, and 0.6:1, respectively. From these observations there is no way of knowing how many females were sexually mature and sexually receptive. It is probably valid to assume that for the three species the proportion of receptive to nonreceptive females was similar. Thus, there were probably many fewer receptive *U. latimanus* females per courting male than in *U. beebei,* with *U. m. terpsichores* falling in between. Crane (1975) has stated that wandering females are sexually receptive. In this study, five of the eight observations of wandering females occurred on days just after the FM. If these females were sexually receptive, then they were synchronizing their reproductive activities with that of the males. However, there have not been any studies correlating wandering activity and ovarian maturity. Several studies have examined ovarian and egg development in relation to lunar phase (von Hagen, 1962, 1970; Feest, 1969; Zucker, 1973). Two of the studies concerning ovarian development (von Hagen, 1962, in *U. tangeri;* Zucker, 1973, in *U. m. terpsichores*) revealed that the ovaries were most highly developed around the FM. However, much individual variation existed. In *U. m. terpsichores* some females exhibited well-developed ovaries during each lunar phase (Zucker, 1973). In *U. m. terpsichores,* at least, males which court at times other than the FM period *(i.e.,* around NM) still have the opportunity of attracting and mating with a sexually receptive female. Von Hagen (1970) showed that females of the seven Trinidad species of *Uca* reach two ovarian maxima: the greatest on days just before the NM, the second on days just before the FM. No indication of differences among the species were given. Males of four of the species showed courtship occurring around both FM and NM. Three of the species showed no distinct rhythm of courtship. Since *U. latimanus* males in the present study almost never engaged in courtship after the NM, it would be interesting to see whether females of this species show only a single ovarian maximum around the FM period with considerably less population variation than the previous studies revealed. These few studies indicate, not surprisingly, that the two sexes are apparently synchronizing their reproductive activities.

The ratio of males to females in a population may influence the degree of synchronization of male courtship. The apparently low ratio of receptive *U. latimanus* females to courting males may be a factor in selecting for the high degree of male synchronous courtship activity revealed in this species. There is some evidence that male courtship not only stimulates females to mate but also stimulates neighboring males to wave in concert and to court more vigorously (Gordon, 1958; Salmon, 1965). The presence of virtually all adult males vigorously courting at one time might insure that the greatest possible number of the relatively few females are stimulated to mate each month. Conversely, the males belonging to the species with the greatest proportion of females (*U. beebei*) showed the least concentration of courtship activities to specific days of the month (Fig. 2). In fact, compared to the other two species, only half as many *U. beebei* males (17%) devoted their time to pure courtship (waving only) (Table II). Apparently, *U. beebei* females could be stimulated to mate with males which invested less time in waving and more in feeding activities than the other two species (Table II). The observations of mated pairs of *U. beebei* on the surface at various times throughout the month also suggests that female specimens of *U. beebei* may show more variability in their time of receptivity and, perhaps, require less premating stimulation *via* courtship. Normally, males must induce females *via* vigorous courtship to follow them into their burrow, where mating typically occurs.

Courtship activities in males and females are highly synchronized and timed to coincide with the spring tides occurring several days following the FM. At this point it is only possible to speculate on the reasons for reproductive activity occurring around the FM rather than during some other lunar phase or environmental event. The availability of food for the resultant larvae has been suggested as the key to the timing of reproduction in annually reproducing marine crabs (Boolootian, Giese, Farmanfarmaian, Tucker, 1959). Seasonal reproduction is apparently not involved in tropical *Uca* since crabs of all sizes (and ages) were observed on the flats throughout the entire year during previous studies (1970–1971, personal observation). Thus, an adequate supply of food must be available throughout the year. However, it is entirely possible that production of the planktonic food sources for larval *Uca* also show cyclic peaks which coincide with the time of *Uca* larval release each month.

A second hypothesis is that mating on days just after the FM insures larval release during the most favorable tides. The most favorable tides should be the highest or spring tides since neap high tides did not always cover the flat. Releasing larvae during the neap tides would require ovigerous females to make a dangerous (?) trek down to the water's edge. According to Feest (1969), larvae of tropical *U. tangeri* and *U. annulipes* are released about two weeks after egg-laying. If the eggs are laid shortly after mating (as Christy, 1978, observed in *U. pugilator*), then they would be ready to be released into the ocean two weeks later, during the following spring-tide period. Likewise, the timing of courtship and the subsequent larval release might provide the larvae with optimal tidal currents several weeks later to transport them back to suitable adult habitats.

Christy (1978) has recently proposed this hypothesis to explain semi-monthly releases of *U. pugilator* larvae off the west coast of Florida. Courtship and mating also peaked twice monthly during the quarter moons (neap tides). Though individual females apparently released larvae only once a month (about two weeks after mating), some did so during each of the quarter moon neap-tide periods. From laboratory studies, he estimated that young crabs would be ready to settle on an intertidal flat about three weeks later, *i.e.*, during spring tides. Spring-tide currents would help ensure up-estuary transport toward suitable adult habitats (Christy, 1978). The same explanation may be true for the three tropical species reported here even though courtship activities are displaced a week from the neap-tide period to the spring-tide period. The warmer waters in Panama as compared to Florida might speed up larval development to the point where young crabs are ready to settle two, rather than three, weeks after release, thus during the next spring tides.

Another possibility is that the timing is not influenced by some requirement of reproduction but rather a requirement of feeding by the adults. The spring tides (when courtship occurs) always coincide with low tides occurring in the late morning, just prior to the noon hour. At this part of the day the substrate is fairly dried out due to the high temperatures, humidity decrease and extreme low tide which thoroughly drains the flat. The dried mud-flat may not be appropriate for efficient feeding (filtering organic matter left on the mud by the ebbing tide). If the crabs are restricted to feeding on the wetter substrate, then courtship would be allocated to mid-day hours, which occur on days just after the NM or FM. Some evidence for this is seen from a previous experiment with *U. m. terpsichores* housed in an outdoor "crabbery" in Panama (Zucker, 1976). The tidal cycles could be manipulated but all other environment factors remained normal (L/D cycles, weather, lunar influence). Crabs maintained on a precise 24 hr tidal cycle with low tide always falling at mid-day and midnight took four weeks to entrain to this tidal cycle, but once they had done so, courtship occurred daily from then on. Crabs maintained on an early morning low-tide period never courted, but fed instead (Zucker, 1976).

All these hypotheses provide explanations for why courtship (and reproduction) should occur around the spring tides. However, there are two spring-tide periods each month, following the NM and the FM. Yet, all three hood-building, Panamanian *Uca* species emphasize the FM spring tides for courtship activities. One spring tide each month is usually more extreme than the other. Every seven months the more extreme spring tide of the month switches (from Tide Tables—USCGS). Over a period of years any given month will have extreme tides after both NM and FM. Thus, there appears to be no particular advantage in timing reproductive activities to either the FM or the NM. The answer to the question of why these *Uca* males court around the FM period must await further studies concentrating on reproduction, both at the level of the crab's behavior in the field and its physiology.

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Summary

1. The degree of synchrony with which three tropical fiddler crabs, *Uca musica terpsichores, U. latimanus* and *U. beebei*, perform courtship, feeding and hood-building activities was studied.

2. Courtship activities cycled on a monthly basis. Significantly more males of all three species courted during the week of the full moon when compared to the

week of the new moon. Virtually no courtship occurred around the quarter moon periods. During peak courtship periods, 78% or more of the males of each species were displaying at the same time.

3. Hood-building also peaked around the full moon and was performed only by courting males. Only a small percentage of courting *U. beebei* males built hoods, while virtually every courting *U. latimanus* male possessed one. An intermediate number of *U. musica terpsichores* built hoods.

4. Almost all of the observed females were feeding. Wandering females (presumably sexually receptive) were observed almost exclusively during the same low tide hours in which males were courting.

5. Both males and females, therefore, appear to be synchronizing and concentrating their reproductive activities to the full-moon period.

Note added in proof

Observations made at LaBoca, Balboa, CZ during July and August 1978 revealed peak courtship occurring during the spring tides following the NM and not following the FM as had been the case during the summer of 1975. This was especially evident in *Uca latimanus*. A check of the 1975 tide tables (USCGS) revealed that the spring tides following the NM were more extreme than those following the FM during the observation period. That is, courtship occurred during the less extreme of the spring tides. In 1978, the reverse occurred, with the extreme tides following the FM. Courtship in 1978, therefore, still took place during the less extreme spring tides, but this time after the NM. This observation lends support to the hypothesis that courtship is timed to permit optimal larval release or larval recruitment back to the flat. Eggs fertilized during the less extreme spring tide period could be ready for release two weeks later during the more extreme tides and/or ready for settling back on the flat four weeks (one lunar cycle) after that. Thus, courtship in these tropical *Uca* appears not to be tied to a particular lunar phase but rather to the less extreme spring tide period each lunar month.

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